A rising tide lifts all phytoplankton: Growth response of other phytoplankton taxa in diatom-dominated blooms

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[1] Oceanic phytoplankton assemblages composed predominantly of picophytoplankton respond to the onset of favorable growth conditions with diatom-dominated blooms, the formation of which involves characteristic growth and accumulation responses by both diatoms and the ambient nondiatom community. Contrary to conventional wisdom, both groups of phytoplankton increase in growth rates and absolute abundance, but the biomass increase of the ambient nondiatom assemblage is modest, especially compared to the order of magnitude or more increase of diatom biomass. This enormous proportional increase in diatom biomass has fostered the misconception that diatoms replace the nondiatom taxa by succession as the bloom matures. However, while the relative abundance of the nondiatom taxa decreases dramatically, their absolute biomass increases modestly and the specific growth rate of picophytoplankton in the bloom increases; at the same time, protistan grazing rate also increases, holding the picophytoplankton assemblage in the bloom to a new steady state biomass concentration. Recent evidence for the ubiquity of the additive response pattern in pelagic diatom blooms comes from observations in many oceanic regions where equatorial upwelling, eddy dynamics, tropical instability waves, and oceanic iron-addition experiments have allowed documentation of the biological response to rapid onset of favorable nutrient, micronutrient or light conditions. The response of diatoms to these favorable conditions is well known; this report offers a more accurate description of the response of the ambient nondiatom taxa to rapid onset of favorable conditions. Realistic representation of the growth dynamics of both the diatoms and nondiatoms in blooms is required to improve forecasting of how future conditions will affect processes that control carbon recycling and export.

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1. Introduction

[2] High biomass diatom blooms are rare, both temporally and spatially, in the world ocean, but they receive a lot of attention from natural scientists because of their commanding ecological and geochemical consequences. Soon after the discovery and identification of diatoms in the Ross Sea in 1847, oceanographers recognized a close association between diatom blooms and rich fish resources [*Gran*, 1912], and that association is now known to be causal because diatom new production fuels the great fisheries [*Ryther*, 1969; *Cushing*, 1989; *Iverson*, 1990; *Smetacek*, 1998]. At the same time, diatom blooms are arguably the marine biological process that has had the largest effect on the variation of radiative properties of Earth's atmosphere in the last 65 million years [*Longhurst*, 1991; *Falkowski et al.*, 1998]. The rise of diatoms co-occurred with the onset of a cooler Earth, the onset of the Bond cycles of cyclic glaciation/deglaciation, and the rise of mammals [*Falkowski et al.*, 2003]. That diatom blooms play a major role in the regulation of atmospheric CO_2 on the geologic time scale is a controversial hypothesis [*Raven and Falkowski*, 1999; *Kohfeld et al.*, 2005; *Broecker and Stocker*, 2006], but one that most carbon cycle researchers agree needs resolution. Furthermore, resolution is now especially critical in view of the current societal need to estimate how anthropogenic changes in radiatively active gases and natural climate variability may interact and feed back through altered oceanic ecosystems to further modify atmospheric CO_2 concentration [*Bopp et al.*, 2003; *Doney et al.*, 2003]. The state of the art in modeling oceanic biogeochemical partitioning is racing ahead with the inclusion of multiple phytoplankton functional groups in ecosystem model components [*Boyd and Doney*, 2002; *Le Quéré et al.*, 2005]. Accurate representation of the perturbation dynamics of a diatom bloom, collapse, and export cycle under future climate conditions is the most demanding component of

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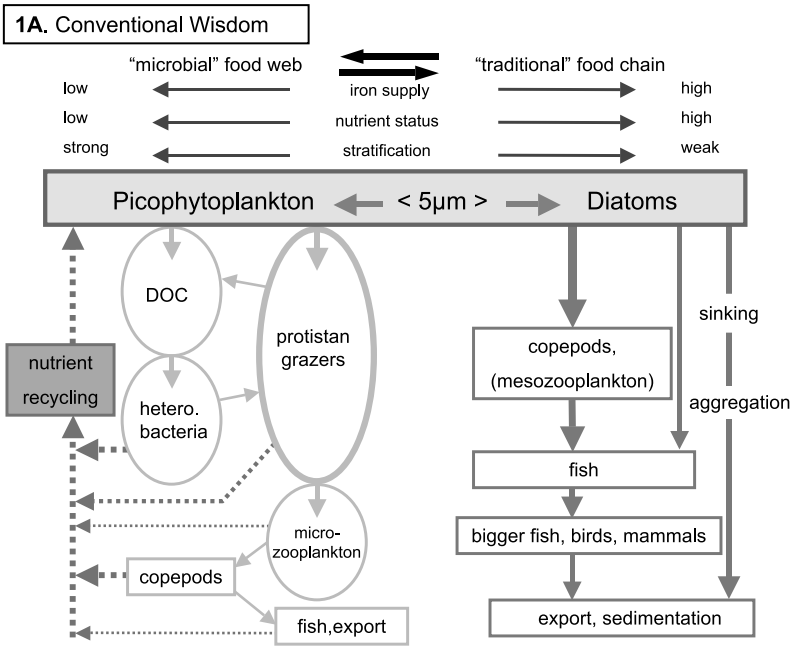

Figure 1a. The conventional view of two-state oceanic food web dynamics, with succession alternating between the microbial loop food web and the traditional diatom-copepod food chain, redrawn from Figure 2 of *Cushing* [1989], who credits *Azam et al.* [1983] for the microbial loop concept. See Table 1 for a chronology of this conventional view of the two-state food web concept. For simplicity the regeneration paths are shown only on the left side of the figure.

multiple functional group representation and requires mechanistic rather than empirical descriptions of the rate processes that drive biomass accumulation and massive export [*Sarmiento et al.*, 2004; *Le Quéré et al.*, 2005; *Sarthou et al.*, 2005; *Veldhuis et al.*, 2005].

[3] Empirical understanding of in situ oceanic bloom dynamics is fairly advanced [*Smetacek*, 1985, 1998; *Kemp et al.*, 2000; *Kiørboe et al.*, 1996; *Sarthou et al.*, 2005]. In the open ocean, the onset of favorable nutrient, light or stability conditions elicits a characteristic response by the ambient phytoplankton assemblages; diatoms, which are initially rare or even undetectable in the ambient assemblage, increase their specific rate of photosynthesis and specific growth rate. Within a few days, as the bloom matures, diatoms comprise the great majority of the bloom biomass [*Landry et al.*, 2000; *Landry*, 2002; *Sarthou et al.*, 2005]. This enormous increase in proportional abundance of diatoms relative to the nondiatom taxa has long been interpreted as replacement of the prebloom taxa by diatoms, or as succession from predominantly nondiatom taxa to diatoms (Figure 1a), and conventional wisdom is that pelagic food webs shift back and forth between two very characteristic structures. Diatoms are assumed to replace the ambient, predominantly picophytoplankton taxa and the change is interpreted as succession in the terrestrial ecological sense defined by *Odum* [1977]. While this interpretation is widely accepted, especially by geochemists and modelers, over the years a few very careful observers, from *Ryther* [1963] to *Landry* [2002], who work in oceanic as opposed to coastal habitats, have quietly noted that there is no replacement of the ambient nondiatom assemblage during diatom bloom formation.

[4] The object of this manuscript is to lay to rest the erroneous concept of phytoplankton taxa replacement in oceanic diatom bloom formation and provide a more accurate description of phytoplankton community structure during such blooms. Observations from a wide variety of recent Joint Global Ocean Flux Study (JGOFS) [*Fasham*, 2003] studies from many oceanic regions from the Southern Ocean to the North Atlantic Ocean can be marshaled to support the thesis we advance, and we will refer to them briefly; however, because of space limitations we will limit this analysis to results from our work in the equatorial Pacific during the EqPac [*Murray et al.*, 1994] and IronEx expeditions [*Martin et al.*, 1994; *Coale et al.*, 1996a] (also F. Chai et al., Modeling responses of diatom productivity and biogenic silica export to iron enrichment in the equatorial Pacific Ocean, submitted to *Global Biogeochemical Cycles*, 2006) (hereinafter referred to as Chai et al., submitted manuscript, 2006).

2. Background

[5] The background versus bloom character of oceanic food webs has long been recognized by researchers who work in the open ocean (Table 1). The conventional interpretation in almost all of the papers included in Table 1 is that there are two phytoplankton assemblages, one predominantly picophytoplankton, the other diatom-dominated, which are alternative food web states, and that

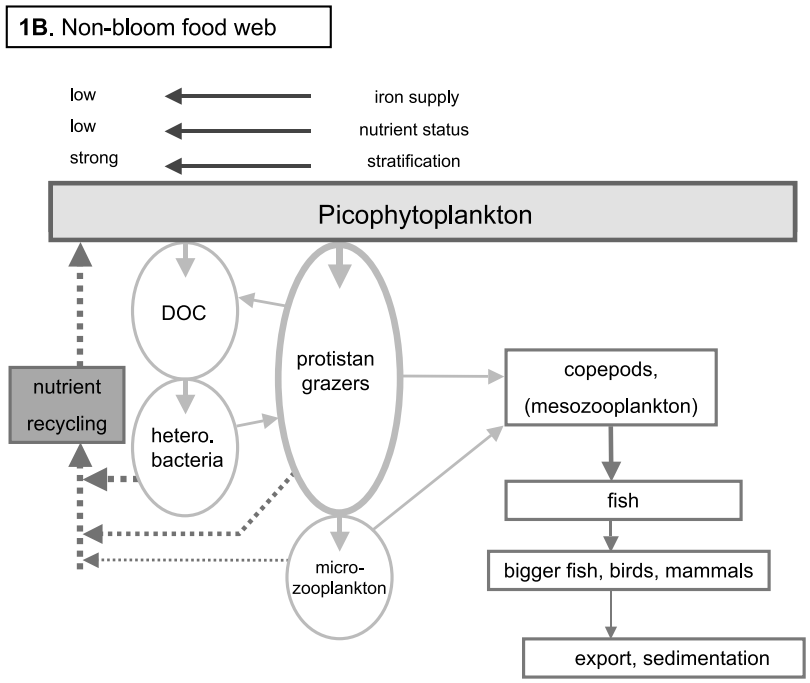

Figure 1b. The oceanic food web dynamics described in this report, showing the ambient predominantly picophytoplankton food web that prevails during oligotrophic conditions. For simplicity the regeneration paths are shown only on the left side of the figure.

environmental growth conditions, favorable or unfavorable, force a transition from one state to the other. In contrast to this two-state concept, there is a parallel concept in aquatic ecology in which the transition back and forth between favorable and unfavorable conditions involves an orderly succession of dominance by various phytoplankton taxa. This sequence is clearly succession, as defined by *Odum* [1977], and it has been recognized for many years in aquatic

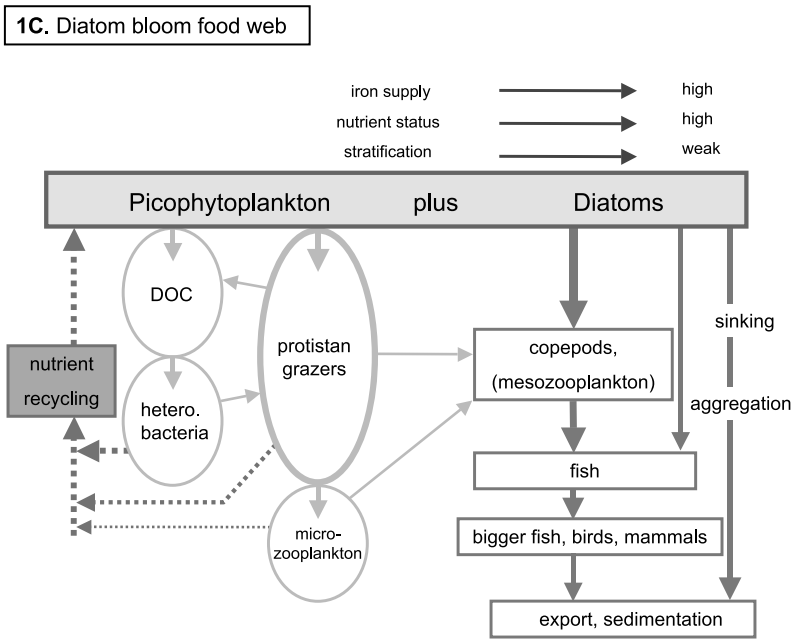

Figure 1c. The oceanic food web dynamics described in this report, showing the complex picophytoplankton and diatom food web structure that prevails in diatom-dominated blooms. For simplicity the regeneration paths are shown only on the left side of the figure.

Table 1. Representative Ideas About the Two-State Character of Open-Ocean Food Webs in Terms of Structure, Forcing and Consequences, Showing That the Two-State Food Web Concept Has Been Recognized Widely, But Interpreted By All But *Ryther* [1963] and *Landry* [2002] as a Replacement or Succession Process, as Illustrated in Figure 1a

Microbial Food Web (Ambient Nondiatom Food Web Assemblage)	Traditional Food Chain (Diatom-Dominated Bloom Food Web)	Reference
	Structure	
Nanoplankton	net phytoplankton	*Yentsch and Ryther* [1959]
Flagellates	flagellates + diatoms	*Ryther* [1963]
Nanoplankton	net plankton	*Malone* [1971]
Dinoflagellates/μzooplankton	diatoms/copepods	*Landry* [1977]
Flagellates	diatoms	*Greve and Parsons* [1977]
Flagellates	diatoms	*Parsons et al.* [1978]
μ-eukaryotes/cyanobacteria	small diatoms (>5μm, <20μm)	*Cushing* [1989]
Picophytoplankton (<5μm)	picophyto. + diatoms (>20μm)	*Landry* [2002]
Protistan grazers	protistan + crustacean grazers	*Landry* [2002]
Picophytoplankton	picophytoplankton + diatoms	this paper, Figures 1b and 1c
	Forcing	
Regenerated nutrients	new nutrients	*Dugdale and Goering* [1967]
Nutrient stress	no nutrient stress	*Greve and Parsons* [1977]
Weakly stratified	strongly stratified	*Cushing* [1989]
No surplus nitrate	surplus nitrate	*Cushing* [1989]
Iron limited	iron replete	*Landry et al.* [1997]
No surplus silicic acid	surplus silicic acid	*Dugdale and Wilkerson* [1998]
	Consequence	
Regenerated production	new production	*Dugdale and Goering* [1967]
Low fish yield	high fish yield	*Ryther* [1969]
Equilibrium	disequilibrium	*Landry* [1977]
Regenerative	renewal	*Wangersky* [1977]
Modest fisheries	the great fisheries	*Cushing* [1989]
Low fish yield	high fish yield	*Iverson* [1990]
Low export	massive export	*Waite et al.* [1992a, 1992b]
Nondiatoms	diatoms	*Dugdale and Wilkerson* [1998]
Efficient recycling	high export	*Dugdale and Wilkerson* [1998]
Balanced biomass	large biomass pulse	*Landry* [2002]
Regenerated production	regenerated + new production	this paper
Recycling	more recycling + export	this paper

settings [*Hutchinson*, 1941]. *Margalef* [1958, 1963, 1978] has provided the most elegant and widely accepted description and explanation of the succession of eukaryotic phytoplankton taxa that occurs in lakes, estuaries and coastal settings where the sediment serves as a reservoir for the resting stages of various, mainly eukaryotic, phytoplankton taxa that participate in this successional sequence. He proposed that succession, driven by a kinetic energy subsidy (wind or tide) that both mixes nutrients upward and keeps diatoms suspended in the euphotic zone, gives diatoms a double growth advantage that allows them to replace nondiatom taxa. When the kinetic subsidy is removed, the opposite causality is at work: Nondiatom taxa replace diatoms, which are now nutrient limited, less buoyant because of nutrient stress, and with no upward kinetic energy subsidy [*Waite et al.*, 1992a, 1992b; *Kiørboe et al.*, 1993, 1996]. In the *Margalef* [1978] model, the nondiatom eukaryotic assemblage that is adapted to low nutrients and strong stratification is a climax condition, the last step in an orderly succession from the ''pioneer'' community of diatoms [*Margalef*, 1967].

[6] On close examination, succession and bloom formation in oceanic habitats appear to be two different processes. *Cushing* [1989, p. 7], after a detailed discussion of physiological mechanisms that may drive succession, as used by Margalef, starts the next section of his paper with the following:

> ''A reasonable generalization might be that there are two main forms of production cycle, that of the spring and autumn outbursts of temperate waters and that of the stratified waters in the oligotrophic ocean and the summer temperate seas. The latter system is in a quasi steady state in which numbers do not change much in time and as a consequence the animals are dispersed. The traditional food chain is based on the high amplitude production cycle with linked production of herbivores and the aggregation of predators.
>
> The production cycle in the oligotrophic ocean is in a quasi steady state and the food chains are long and the organisms are dispersed. The great fisheries of the world are based on the traditional food chain, rooted in the small diatoms (>5 μm in diameter) and their successors in the spring outburst and, in the upwelling areas, the larger flagellates.''

Cushing's [1989] separation of succession from the two-state ''production cycle'' encourages us to proceed with an analysis of the oceanic two-state transition process. We believe the ideas presented here are not in conflict with the conventional successional hypothesis of aquatic ecology, but stress that the oceanic transition from the ambient

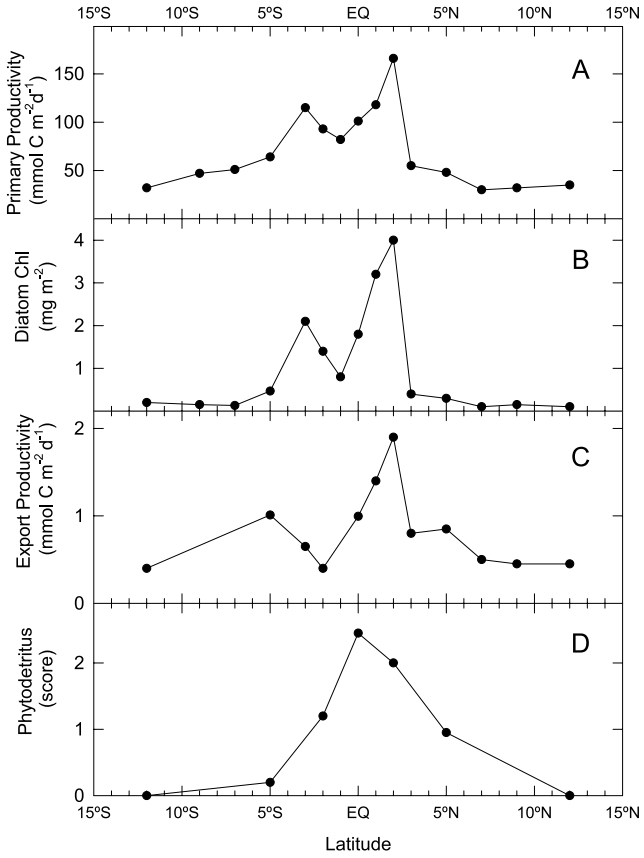

Figure 2. Covariation of four properties related to diatom growth, export, and burial on a meridional transect across the equator along 140°W longitude from 12°S to 12°N in the Pacific Ocean during August and September 1992. (a) Primary productivity from *Barber et al.* [1996]; (b) diatom biomass from *Bidigare and Ondrusek* [1996]; (c) carbon export flux from *Murray et al.* [1996]; (d) phytodetritus on the sea floor from *Smith et al.* [1996]. The maximum in primary productivity, diatom biomass, and export productivity at 2°N was associated with the cold side of an instability wave front [*Johnson*, 1996; *Archer et al.*,1997; *Barber et al.*, 1996], which was visible from space [*Yoder et al.*, 1994].

oligotrophic assemblage to a high-biomass bloom does not appear to be succession in the sense that Margalef uses the term.

[7] The large proportional increase in diatom biomass that characterizes bloom formation has led most, but not all, of the authors cited in Table 1 to the interpretation that diatoms replace the nondiatom taxa. Before we show why we believe that interpretation is erroneous, consider a comment by *Ryther* [1963, p. 25] (our italics):

> "What we find in Bermuda [at the oceanic Bermuda hydrographic station] are two kinds of communities. One is a community which is adapted to living under very poor conditions, inhabited by small flagellates which are able to swim around and snap up an occasional phosphate ion, and so on. They make their own vitamins, and they are adapted to living under very unfavorable conditions, it seems. Then, there is another community which suddenly appears when there is a turnover and the water is richer and there are vitamins present. These diatoms can grow very rapidly, and they are used to living in lush conditions. They can outgrow or outstrip the other. Although the little flagellates hang on, they can never grow as fast, apparently, as the diatoms. It looks, therefore, as though they were being selected against, but, really, *they are just staying at the same level all the time, and the diatoms come in and go out again*."

Ryther [1963] clearly had a good intuitive sense of the additive nature of bloom formation. More recently, *Landry* [2002, p. 32] makes the identical point while commenting on EqPac and IronEx results (our italics):

> "Phytoplankton biomass is further increased in this food web by adding more limiting nutrient, as was done during the IronEx II fertilization (Figure 4). The result was a >40-fold increase in the biomass of microphytoplankton (>20-μm size fraction), with a largely negligible effect on smaller cells [*Landry et al.*, 2000]. Such observations define the order in which *successively larger phytoplankton are added to the food web* by 'overprinting' its relatively stable base of small cells [e.g. *Chisholm*, 1992; *Landry et al.*, 1997]."

3. Strategy and Methods

[8] The analysis presented here is based on work in the equatorial Pacific in wind-driven equatorial upwelling, tropical instability waves and other processes involving frontal dynamics that often produce favorable conditions for the beginning of a diatom bloom. In the fall of 1992 during onset of a cool ENSO phase [*Murray et al.*, 1994], there were numerous manifestations of short-lived diatom blooms driven by equatorially trapped processes that upwelled nutrient-rich water [*Lindley et al.*,1995; *Barber and Chavez*, 1991; *Bidigare and Ondrusek*,1996; *Landry et al.*, 1996; *Latasa et al.*, 1997]. These equatorial waters are rich ($\gg K_s$) in nitrate and phosphate and have highly variable diatom abundance [*Chavez et al.*, 1990, 1996]. The limiting nutrients provided to the euphotic zone by these physical processes were likely iron [*Coale et al.*, 1996b], silicic acid [*Dugdale and Wilkerson*, 1998], or both. Figure 2 shows the increase of primary productivity and diatom abundance at 2°N on a meridional section across the equatorial waveguide at 140°W. Productivity, diatom abundance, and particle flux through the 100-m-depth horizon are all maximal at 2°N where an instability front brought the iron-rich Equatorial Undercurrent into the euphotic zone [*Barber et al.*, 1996; *Johnson*, 1996; *Archer et al.*, 1997; *Foley et al.*, 1997]. The euphotic zone diatom maximum close to 2°N was associated with a maximum of fresh phytodetritus on the sea floor about 4000 m below. This September 1992 bloom at 140°W was so dense that it was visible to the space shuttle crew the same week we sampled the front [*Yoder et al.*, 1994; *Archer et al.*, 1997; *Barber et al.*, 1996]. *Kemp and Baldauf* [1993] have described laminated diatom deposits in the equatorial Pacific that look as though they could have been laid down by a frontal bloom similar to the one we observed in 1992.

[9] Analyses of pigment composition on equatorial transects in fall 1992 showed strong equatorial maxima in total chlorophyll and diatom chlorophyll with no decrease in prokaryotic chlorophyll [*Bidigare and Ondrusek*, 1996,

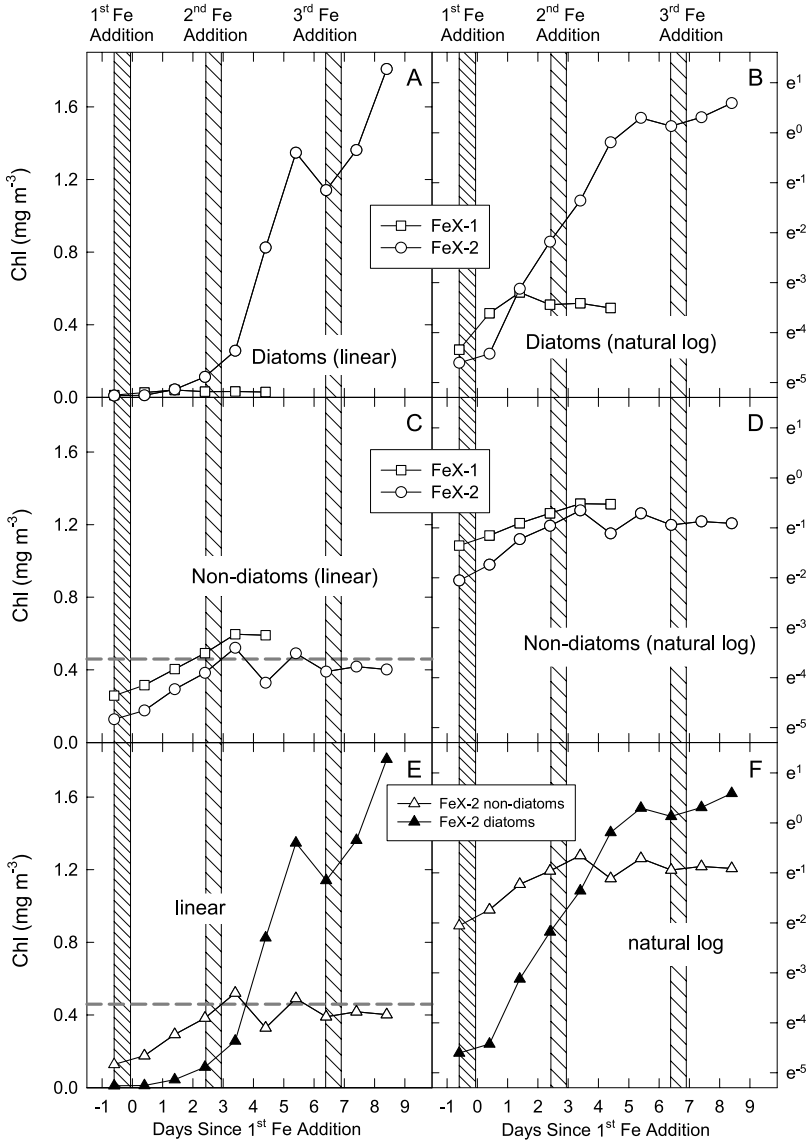

Figure 3. Time series of the increase of (a, b) diatom and (c, d) nondiatom chlorophyll following addition of iron in the 1993 IronEx-1 [*Martin et al.*, 1994] and 1995 IronEx-2 [*Coale et al.*, 1996a; *Landry*, 2002] in situ Fe addition experiments in the eastern equatorial Pacific Ocean. (e, f) Time series of chlorophyll change in IronEx-2 for both diatoms and nondiatoms in one graph. Time series are shown in both linear (Figures 3a, 3c, and 3e) and natural log (Figures 3b, 3d, and 3f) chlorophyll units to demonstrate different quantitative aspects of the initial responses to iron addition. The dashed lines in Figures 3c and 3e represent the new equilibrium chlorophyll value ($B_{new} \approx 0.46$ mg Chl m^{-3}) for the IronEx-2 nondiatom assemblage from Day 2.4 to Day 9.4. The vertical bars with diagonal lines show when iron was added: once in IronEx-1 (fine diagonal lines), and three times in IronEx-2 (fine and thick diagonal lines). Robert R. Bidigare (University of Hawaii) provided the phytoplankton pigment data, which were determined by HPLC [*Bidigare and Ondrusek*, 1996] and converted to chlorophyll associated with various taxa using pigment equations from *Letelier et al.* [1993].

Figures 8 and 9]. *Landry et al.* [1996, p. 871] show similar data from equatorial transects and summarize their observations, "Picoplankton account for most of the chlorophyll biomass and primary production in the central equatorial Pacific. Nonetheless, their abundances and distributions are relatively stable and conservative while other populations, such as diatoms, respond more dramatically to environmental forcing."

[10] Quantifying growth responses driven by a natural enrichment transient is difficult. The spatial and temporal expressions of complex processes such as instability waves [*Johnson*, 1996] make it hard to determine when and where the enrichment started. To overcome this difficulty we have

Fe Addition	Day	Net μ_{chl} (d^{-1}) Diatoms	Non-diatoms	Cyanophytes + prochlorophytes
		IronEx-1		
1st	-0.6			
	0.4	0.73	0.27	0.01
	1.4	0.42	0.38	0.27
	2.4	-0.24	0.22	0.27
	3.4	0.03	0.07	0.27
	4.4	-0.10	-0.01	-1.52
	4-day mean	*0.24*	*0.24*	*0.21*
		IronEx-2		
1st	-0.6			
	0.4	1.32	0.74	N.D.
	1.4	0.95	0.30	0.42
2nd	2.4	0.82	0.31	0.25
	3.4	1.17	-0.51	-0.08
	4.4	0.49	0.56	0.30
	5.4	-0.17	-0.48	-0.29
3rd	6.4	0.18	0.10	0.18
	7.4	0.28	-0.44	-0.32
	8.4	-0.01	0.68	0.00
	4-day mean	*1.07*	*0.21*	*0.19*

Figure 4. Net chlorophyll-specific rate of increase, μ_{chl} (d^{-1}), of diatom, nondiatom, and cyanophyte plus prochlorophyte chlorophyll in the IronEx-1 [*Martin et al.*, 1994] and IronEx-2 [*Coale et al.*, 1996a] experiments. Values are calculated for daily intervals according to equation (5) of *Kirchman* [2002] from HPLC pigment data provided by R. Bidigare (U. Hawaii) [*Bidigare and Ondrusek*, 1996]; they are equivalent to the slopes of the chlorophyll time series in the natural log graphs of Figure 3. Dotted lines show when iron was added, once in IronEx-1 and three times in IronEx-2. Italicized values are mean net μ_{chl} (d^{-1}) values for the first 4 days in each experiment.

analyzed the results of two iron addition experiments, IronEx-1 [*Martin et al.*, 1994] and IronEx-2 [*Coale et al.*, 1996a], where the time and place of the enrichment were controlled, making it possible to construct precise time series analyses. *Lindley and Barber* [1998] found that the ambient phytoplankton response in the naturally iron-rich island wake of the Galapagos Islands was virtually identical to the biological response in the IronEx experiments. On the basis of these observations we propose that the open-ocean iron experiments are good surrogates for natural enrichment transients.

[11] The observations in Figures 3 and 4 on the abundance and chlorophyll-specific net growth rate of diatom, nondiatom, cyanophyte and prochlorophyte taxa were determined by high performance liquid chromatography (HPLC) pigment analyses done by *Bidigare and Ondrusek* [1996]; pigment analyses were converted to chlorophyll associated with various taxa using pigment equations of *Letelier et al.* [1993]. Samples for HPLC analysis were collected from the surface and immediately filtered; the filters were placed in liquid N_2 for later HPLC analysis back at the lab. The time series of photochemical efficiency (Figure 5) was determined by Fast Repetition-Rate Fluorometry (FRRF) on 3-m water samples at frequent intervals in the iron-enriched waters [*Kolber et al.*, 1994; *Behrenfeld et al.*, 1996]. Together the HPLC and FRRF analyses are a suite of well-resolved spatial and temporal observations.

4. Diatom Response

[12] Diatom bloom initiation at onset of favorable environmental conditions is probably the most studied phenomenon in oceanography [*Gaarder and Gran*, 1927; *Riley*, 1946; *Sverdrup*, 1953; *Ryther*, 1969; *Dugdale and Wilkerson*, 1998; *Hiscock et al.*, 2003; *Sarthou et al.*, 2005]. It has commanded much attention because of the well-established relationship between diatom blooms and fish production [*Iverson*, 1990], which led Bostwick Ketchum to revise Isaiah 40:6 this way, "All fish is diatom." Together with the fish connection, diatom blooms are a major biological process for regulating the concentration of CO_2 in Earth's atmosphere. Although it is prudent to say the preceding statement is a hypothesis that is controversial, few oceanographers would deny that the formation of massive diatom blooms and their termination by rapid sinking to the sea floor have the potential, over geological timescales, to modify the partitioning of carbon in the atmosphere-ocean-sediment system. The sedimentary record indicates that massive episodic burial has taken place [*Kemp and Baldauf*, 1993].

[13] Although the environmental forcing of the diatom growth response is well understood, we will describe

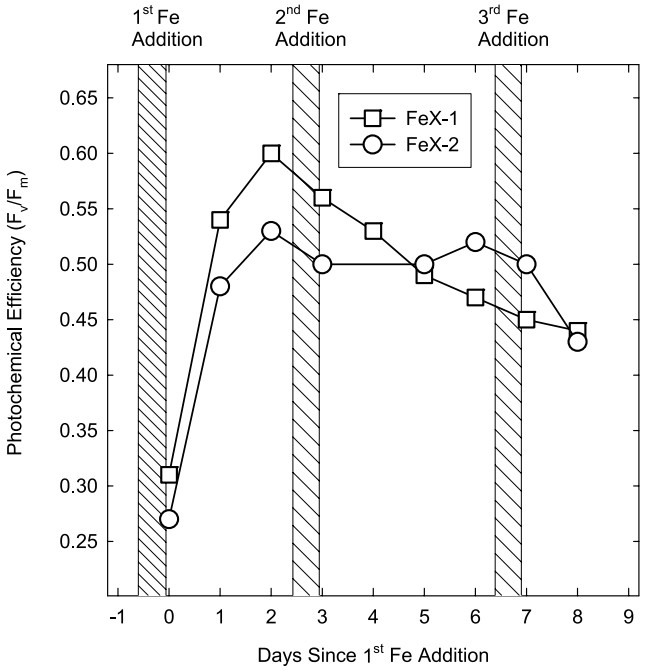

Figure 5. A time series of photochemical efficiency (F_v/F_m) in IronEx-1 and IronEx-2. F_v/F_m was determined with a Fast Repetition Rate Fluorometer (FRRF). The vertical bars with diagonal lines show when iron was added: once in IronEx-1 (fine diagonal lines), and three times in IronEx-2 (fine and coarse diagonal lines). F_v/F_m data for IronEx-1 are from *Kolber et al.* [1994] and, for IronEx-2, from *Behrenfeld et al.* [1996].

several aspects of it as they relate to our thesis. The response of diatoms in IronEx-1 was quite different from that in IronEx-2 [*Martin et al.*, 1994; *Coale et al.*, 1996a; *de Baar et al.*, 2005; *Tsuda*, 2005] (Figures 3a and 3b). The ambient diatom abundance in both experiments was initially low and similar (0.013 mg chl m^{-3} in IronEx-1; 0.010, in IronEx-2), making up about 5% of the chlorophyll biomass of the ambient phytoplankton assemblage. In the linear plot in Figure 3a there is no detectable diatom response to iron addition in IronEx-1, but the natural log plots in Figure 3b and the chlorophyll-specific net growth rates (μ_{chl}) in Figure 4 indicate that in IronEx-1 diatoms initially responded to iron addition and had a net growth rate of $\mu_{chl} = 0.73\ d^{-1}$ during the first day after iron addition. In the second day the diatom rate decreased to $\mu_{chl} = 0.42\ d^{-1}$, and on the third day μ_{chl} was negative (Figures 3b and 4). That no significant diatom bloom took place in IronEx-1 was an unusual response when considered in the context of the eight subsequent iron addition experiments [*de Baar et al.*, 2005], all of which elicited well-defined diatom blooms. The cause of the failure to develop a diatom bloom has been the subject of much discussion [*Martin et al.*, 1994; *Coale et al.*, 1996a; *Landry et al.*, 2000; *de Baar et al.*, 2005]. The general assumption is that multiple iron additions in IronEx-2 were responsible for the massive diatom bloom and that IronEx-1 simply ran out of iron before a diatom bloom got started, but the results described above are inconsistent with this assumption. The diatom net growth rate and chlorophyll concentration increased dramatically in both iron addition experiments on the first day, and this initially positive response was followed by dramatically different trajectories between the two diatom assemblages well before the second iron addition in IronEx-2 (Figure 3b).

[14] For the first 24 hours following the first iron addition of IronEx-2, the diatom net μ_{chl} was $1.32\ d^{-1}$, and on the second day it was $0.95\ d^{-1}$. The mean net μ_{chl} for the first 2 days was $1.14\ d^{-1}$ versus a 2-day mean of diatom net $\mu_{chl} = 0.58\ d^{-1}$ in IronEx-1. The IronEx-2 diatoms went on to maintain a mean net μ_{chl} rate for the first 4 days of $1.07\ d^{-1}$, a very high net growth rate for a pelagic bloom. IronEx-1 diatoms had a mean net μ_{chl} rate for the first 4 days of $0.24\ d^{-1}$. After Day 3.4 during IronEx-2 the μ_{chl} decreased but remained positive, and from Day 4.4 to Day 8.4 the diatom biomass increased to >1.6 Chl m^{-3}. The diatom accumulation in IronEx-2 is impressive, but it has been duplicated in several other iron addition experiments and even exceeded in a North Pacific iron addition experiment [*de Baar et al.*, 2005; *Tsuda*, 2005].

[15] The short IronEx experiments did not provide a clear opportunity to document the collapse of a high biomass diatom bloom and the removal of the diatom "overprinting" (Figure 1c) from the ambient nondiatom assemblage (Figure 1b). There is, however, a wealth of observations on bloom collapse. During the first few days of IronEx-2, diatom accumulation was initially uncoupled from grazing losses and biomass accumulated exponentially. Such fast growing diatoms under optimal conditions regulate their buoyancy and virtually shut down losses due to sinking. Chlorophyll concentrations of 5 to 30 mg Chl m^{-3} accumulate in blooms under conditions of high growth rates and buoyancy regulation [*Kiørboe et al.*, 1993, 1996; *Waite et al.*, 1992a, 1992b]; the September 1992 diatom bloom we observed at 2°N had surface concentrations of 30 mg Chl m^{-3} on one side of a subduction frontal system [*Johnson*, 1996; *Archer et al.*, 1997].

[16] Such high biomass diatom blooms quickly deplete the new nutrients or micronutrients provided by the physical process. Onset of nutrient depletion renders the diatoms physiologically incapable of regulating buoyancy [*Waite et al.*, 1992a, 1992b] and they often release sticky polymers, causing aggregation of the increasingly dense cells [*Alldredge et al.*, 1995]. Massive fluxes of diatoms can take place, with an entire population sinking out of the euphotic zone in a matter of hours [*Kemp et al.*, 2000; *Sancetta et al.*, 1991; *Smetacek*, 1985]. While aggregation and massive export flux are the most spectacular means by which a dense diatom bloom can collapse, the other fate of a dense bloom is for grazers, through reproduction, to catch up to the autotrophic accumulation and quickly graze the diatoms back to the pretransient level [*Landry et al.*, 2000; *Landry*, 2002].

5. Nondiatom Response

[17] The response of the ambient nondiatom, predominantly picophytoplankton assemblage to the addition of iron was rapid and dramatic in both IronEx experiments. Within a half day after the completion of iron addition, nondiatom biomass had increased detectably (Figures 3c and 3d). Tight coupling between onset of favorable conditions and rapid increases in photochemical efficiency, net growth rates, and biomass are characteristic of the ambient nondiatom assemblage in the equatorial Pacific [*Kolber et al.*, 1994; *Landry et al.*, 1996, 2000; *Foley et al.*, 1997; *Landry and Kirchman*, 2002]. In IronEx-2 the initial nondiatom chlorophyll concentration was 0.13 mg Chl m^{-3}, about half the initial concentration in IronEx-1; the gap in biomass was closed in the first day after iron addition and further increases in chlorophyll and net μ_{chl} were remarkably similar in the two experiments. In both, nondiatom chlorophyll increased at a modest exponential rate to concentrations of about 0.4 to 0.6 mg Chl m^{-3}, roughly a tripling of the initial nondiatom chlorophyll concentration. The mean net μ_{chl} was $0.24\ d^{-1}$ in IronEx-1 and $0.21\ d^{-1}$ in IronEx-2 for the first 4 days (Figure 4). After the rapid initial increase there was no further increase because, as *Landry et al.* [2000] have shown, the protistan grazers of the microbial food web also increased in abundance and grazing rates in both experiments. The balance between net growth and grazing loss prevented a large accumulation of nondiatom biomass [*Landry*, 1977; *Landry et al.*, 1997; *Landry*, 2002]. During the favorable growth transient, the autotrophs and their protistan grazers shift to higher, but still balanced, biomass and rate levels as described in the following equations, after *Lindley et al.* [1995]. In the balanced microbial food web:

$$\frac{dB}{dt} = (\mu - m)B = 0 \tag{1}$$

$$\mu = m, \tag{2}$$

where B is autotrophic picophytoplankton biomass, μ is its specific growth rate, and m is the specific mortality loss rate due to the sum of all loss processes. Since the majority of loss in the microbial food web is due to grazing, we refer to the sum of the losses as grazing loss. The balance between autotrophic growth rate and grazing (loss) rate requires that m is density dependent,

$$m = aB. \tag{3}$$

At steady state, the (loss) grazing constant a can be defined. Since $\mu = m$,

$$\mu = aB \tag{4}$$

$$\frac{\mu}{a} = B. \tag{5}$$

Under the influence of the favorable transient, μ increases to μ_{new} and biomass increases proportionally to B_{new},

$$\frac{\mu_{new}}{B_{new}} = a. \tag{6}$$

For the duration of the favorable transient, then, this relationship predicts a higher steady state biomass, increased steady state growth rate of small autotrophs, plus increased grazing loss rate (m_{new}) [*Lindley et al.*, 1995; *Landry and Kirchman*, 2002]. Protistan grazers in pelagic food webs are almost always capable of preventing the formation of high biomass blooms of picophytoplankton; we know of only two reports of picophytoplankton blooms >1.5 mg chl m^{-3} in the open ocean [*Morel*, 1997; *Bidigare et al.*, 1997].

[18] In IronEx-1 and IronEx-2, nondiatom assemblages reached the shifted-up biomass levels (B_{new}) quickly. In IronEx-1 the iron-enriched parcel of water subducted beneath a layer of water with ambient (low) iron concentrations between Day 4 and Day 5; therefore, the surface HPLC pigment values after Day 4 are not representative of the iron-stimulated community, making it impossible to determine B_{new} for IronEx-1 with any confidence. Figures 3c and 3d suggest that the nondiatom assemblages in the two experiments were following similar trajectories. In IronEx-2 the mean B_{new} value (0.46 mg Chl m^{-3}) was reached between Day 1.4 and Day 2.4, and was maintained for at least 8 days with an oscillation of values between Days 2.4 and 6.4 (Figure 3e) that suggested protistan grazers and autotrophs were settling into the new B_{new} equilibrium value through a series of damped oscillations.

[19] Chlorophyll-specific net growth rate calculations for cyanophyte and prochlorophyte chlorophyll indicated that the nondiatom response was representative of the prokaryotic picophytoplankton response (Figure 4). For the first 4 days of IronEx-1 the mean nondiatom net $\mu_{chl} = 0.24\ d^{-1}$, the cyanophyte and prochlorophyte net $\mu_{chl} = 0.21\ d^{-1}$; in IronEx-2 the net μ_{chl} values were similarly close, net $\mu_{chl} = 0.21\ d^{-1}$ for nondiatoms and $0.19\ d^{-1}$ for cyanophytes and prochlorophytes. These results confirm that the iron response of the two major prokaryotic groups is similar to the bulk nondiatom assemblage iron response; that is, they increased modestly in both biomass and chlorophyll-specific net growth rate as also reported by *Mann and Chisholm* [2000].

[20] Analysis of photochemical efficiency with the Fast Repetition Rate Fluorometer (FRRF) has provided surprising results from the two IronEx experiments (Figure 5). FRRF observations in IronEx-1 and IronEx-2 show that ambient F_v/F_m values in the equatorial Pacific are very low, around $F_v/F_m = 0.3$, indicating that ambient picophytoplankton were iron limited when the IronEx experiments were carried out (Figure 5). After iron addition in both experiments, F_v/F_m increased to high values in the first 24 hours and up to maximal values after 48 hours. The IronEx-1 and IronEx-2 response curves of photochemical efficiency versus time were similar. In both experiments the phytoplankton assemblage in the first 24 and 48 hours was composed almost entirely of small phytoplankton. When the massive diatom accumulation did develop in IronEx-2, the F_v/F_m curve remained similar to the response curve of IronEx-1 where no diatoms were present.

6. Discussion

[21] The obvious questions generated by this analysis are (1) why is there no replacement of picophytoplankton by diatoms when a physical or chemical transient abruptly provides favorable growth conditions, and (2) is this significant? First, why is there no succession or competitive exclusion if the two groups are competing for a single limiting nutrient (iron) and other resources (light and macronutrients) are not limiting [*Huisman and Weissing*, 2000, 2001]? Why do diatoms "overprint" the background picoplankton rather than replace them? To understand this, it is helpful to examine the strengths and inconsistencies of conventional wisdom. The essence of the discussion on the interactions between these two phytoplankton groups by *Morel et al.* [1991], *Chisholm* [1992], *Raven* [1998], and many others (Table 1) is well summarized in the Ecumenical Hypothesis. The Ecumenical Hypothesis [*Morel et al.*, 1991] states that large phytoplankton cells are more vulnerable to iron limitation than are picophytoplankton and that this vulnerability accounts for the dominance of picophytoplankton in iron poor oceanic settings. Morel and his coauthors hypothesize that the photochemical efficiency of picophytoplankton is less sensitive to low iron rations because small cells have lower cell quotas for iron, and lower half saturation constants for iron uptake enable them to take up iron rapidly at low concentrations [*Price et al.*, 1994]. More importantly, the Ecumenical Hypothesis predicts that after iron addition the photochemical efficiency and growth rate of ambient picophytoplankton in high nutrient low chlorophyll (HNLC) waters will not increase much because the small cells are not strongly iron limited and do not have the ability to respond to high levels of iron availability by increasing photochemical efficiency. In contrast, after iron addition large diatoms are predicted to show large increases in photochemical efficiency and growth rate because, with higher values of maximal uptake (V_{max}) and maximal growth rate (μ_{max}) for iron [*Coale et al.*, 1996b],

they can effectively exploit the newly available iron concentrations (~4 nM) provided by iron addition experiments [*Coale et al.*, 1996a; *de Baar et al.*, 2005].

[22] However, large diatoms are initially very rare (Figure 3) and it takes several days for them to accumulate a significant biomass following iron addition. If the bulk increase in photochemical efficiency resulting from iron addition is being driven by the diatom response, as stated in the Ecumenical Hypothesis, the increase should start slowly and increase as diatoms begin to dominate the bloom's taxonomic composition. In situ FRRF observations of photochemical efficiency during both IronEx-1 and IronEx-2 [*Kolber et al.*, 1994; *Behrenfeld et al.*, 1996] are inconsistent with the Ecumenical Hypothesis; instead, the FRRF results show that photochemical efficiency increased to maximal values during the first day of each experiment (Figure 5). We interpret this to indicate that the ambient, picophytoplankton were initially strongly iron limited and physiologically capable of using the newly available iron. In addition, the IronEx-1 result, where only picophytoplankton responded to iron addition (Figure 3), shows that the rapid rate increase persisted for a week or longer in the picophytoplankton dominated assemblage (Figure 5). Awareness of this initial strong positive response of ambient picophytoplankton to iron addition (Figure 5) is critical to understanding why diatoms do not displace picophytoplankton.

[23] When iron suddenly becomes available in saturating concentrations the two groups compete for available iron. Individual diatoms can take up iron that is present at saturating concentrations much faster than picophytoplankton, but initially there are so few diatoms (Figure 3) that, as a population, they take up only a trivial proportion of the total available iron. In contrast, the uptake systems of the picophytoplankton are saturated at their lower maximum uptake rates, yet most of the iron is initially partitioned into picophytoplankton because of their overwhelming biomass dominance. As shown previously, the iron-limited ambient picophytoplankton increased their photosynthetic efficiency within hours of iron addition (Figure 5). With excess iron available and saturated uptake rates, the ambient assemblage of picophytoplankton shifts up to a new, higher growth rate (μ_{new}) (equation (6)), but because of efficient micrograzing losses they cannot accumulate enough biomass to take up enough new iron to prevent the rapidly increasing diatoms from eventually taking up most of the iron. At the end of the bloom, in terms of photosynthetic efficiency, picophytoplankton are healthier than they were before iron addition, but over the course of the bloom their bulk impact on the newly available iron is small. The key issue is that as the bloom progresses, neither group outcompetes the other: Picophytoplankton abundance is limited by micrograzers, and diatoms compete with themselves. Picophytoplankton get all the iron they need to grow at maximal rates; still, diatoms monopolize most of the newly available iron. When diatom uptake drives down iron concentration to diatom rate limiting concentrations, picophytoplankton, with lower k_s values, are able to drive iron concentration still lower. As the iron transient decays to background concentrations, ecological theory predicts that picophytoplankton with a lower requirement for iron very effectively displace diatoms from the ambient assemblage [*Huisman and Weissing*, 2000, 2001].

[24] As to the second question generated by this analysis, is the paradigm change presented here quantitatively significant for carbon cycle modeling? *Landry et al.* [2006] argues that the increase in microbial cycling during blooms merits attention from modelers; his work in a variety of ocean settings as well as that of *Eppley et al.* [1979] indicates that bloom microbial production, grazing and respiration can be enhanced several fold over background carbon cycling by this food web. A novel attempt at parameterizing the microbial food web was carried out by *Denman and Peña* [2002] and *Denman* [2003] using the suggestion of *Steele* [1998] for including the picoplankton/micrograzer loop in an ocean ecosystem model of conditions at Ocean Station P in the subarctic North Pacific Ocean. Several "climate change" scenarios including the removal of iron limitation were run to examine how the microbial loop dynamics responded during the spring bloom. Not surprisingly, the iron-enhanced run showed a 29% increase in export flux across the 50-m-depth horizon from about 0.8 mol N m^{-2} yr^{-1} to about 1.0 mol N m^{-2} yr^{-1}. In contrast, the export ratio, defined as the flux through the 50-m depth divided by total primary productivity, decreased in the iron-enhanced treatment; with iron limitation the export ratio was 0.46, while in the iron-enhanced scenario it decreased 32% to about 0.31. If absolute export flux increased with iron but the export ratio decreased by a third, there was a significant increase in recycling with iron. Direct flux measurements from the Southern Ocean iron addition experiment [*Buesseler et al.*, 2005] appear to confirm the *Denman* [2003] model result: the absolute export flux increased with iron but the export ratio decreased during the peak of bloom formation. These field and model results suggest that the new paradigm may contribute to improved carbon cycle models.

[25] The concept advanced here is also pertinent to the 15-year controversy sparked by *Martin*'s [1990] Iron Hypothesis [*Chisholm*, 1995]. Among other issues, this debate concerns the important environmental question, will engineered iron fertilization cause irreversible changes in the pelagic ecosystem? Producing a strong export response to iron enrichment requires both initial HNLC conditions and a low background abundance of mesozooplankton, which allows diatom biomass to initially accumulate faster than ambient mesozooplankton can consume it [*Landry et al.*, 2000]. Continuous iron fertilization will not produce efficient sequestration of carbon because as the mesozooplankton become abundant they can continuously graze and recycle a large proportion of the newly produced diatom biomass in the surface layer. This increased grazing rate prevents the accumulation of the diatom biomass needed for efficient export. Therefore, efficient engineered carbon sequestration requires episodic Fe enrichment with a return to the ambient picoplankton-dominated assemblage between enrichments.

[26] Furthermore, iron enrichment drives consumption of N, P and Si much faster than open ocean physical processes can resupply macronutrients (Chai et al., submitted manuscript, 2006), so continuous iron fertilization cannot effi-

ciently sequester carbon because the required HNLC conditions are not reestablished. Despite their ability to exploit nutrient transients, picophytoplankton are specialized for competition in resource limited environments [*Raven*, 1998]. Both ecological theory [*Huisman and Weissing*, 2000, 2001] and modeling (*Chai et al.*, submitted manuscript 2006) indicate that an iron-driven diatom bloom necessarily forces an oscillation back to a picophytoplankton-dominated assemblage, indicating that engineered iron fertilization will not force an irreversible change in pelagic ecosystems to either continuous diatom blooms or continuous picophytoplankton dominance.

7. Conclusions

[27] Diatoms at very low abundances and the ambient predominantly picophytoplankton assemblages of oligotrophic open-ocean regions both respond positively to onset of favorable growth conditions. Diatoms grow fast, reduce sinking loss by increasing buoyancy, and for a few days accumulate biomass faster than the mesozooplankton grazers can consume it. The picophytoplankton-protistan food web shifts to higher autotrophic growth rates and biomass levels, but grazing also increases, so balance is maintained and accumulation of picophytoplankton biomass is limited. New, slightly higher, equilibrium values of μ_{new}, B_{new}, and m_{new} are maintained in the microbial food web as long as the favorable conditions persist.

[28] Nondiatom autotrophs, especially picophytoplankton, are more abundant in diatom blooms than in ambient, prebloom assemblages under oligotrophic conditions. The microbial food web in a bloom is more important quantitatively to the carbon cycle than it is during background steady state conditions. There is more absolute recycling of carbon back to CO_2 under bloom conditions than under nonbloom conditions, notwithstanding that carbon export exceeds recycling by many fold in the bloom process.

[29] Diversity and food web complexity are higher in the episodic bloom than in the background steady state food web. The big biomass winners, the diatoms, do not replace the ambient picophytoplankton assemblage; therefore there is no succession in the ecological sense of the term during bloom cycles.

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